

POSTPALEOZOIC HISTORY OF THE SILICEOUS SPONGES WITH RIGID SKELETON

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Most of the Mesozoic groups of siliceous sponges with rigid skeletons (Hexactinosa, Lychniscosa and 'Lithistida') have Paleozoic roots, except the Lychniscosa known from the Middle Jurassic to Recent, and the 'lithistid' *Didymorina* known only from the Jurassic. The Triassic record of these groups is poor, and all become common only in the Middle - Late Jurassic, but probably reach maximum diversity and frequency during the Late Cretaceous. The Tertiary record of all these groups is much poorer than for the Mesozoic. Hexactinosa and 'Lithistida' are common elements of Recent deeper water faunas, while Lychniscosa, which were very common during the Mesozoic, are very rare and of low diversity in modern seas. Known and newly discovered Tertiary faunas show many affinities with Cretaceous ones indicating lesser susceptibility of these sponges to K/T boundary disturbances, than seen in other organisms. Large faunas of siliceous sponges with rigid skeletons occur in the fossil record in a punctuated manner, and are correlated with high sea level stands. □ *Porifera, Hexactinosa, Lychniscosa, Lithistida, PostPaleozoic history, K/T boundary.*

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Siliceous sponges with rigid skeletons are virtually the only ones which have sufficient fossil records to allow some generalisations to be deduced about their history and patterns of distribution during the Mesozoic. Here belong the Hexactinosa, Lychniscosa and the polyphyletic assemblage we currently know as 'Lithistida'. Even these records, however, are very punctuated. Sponges with skeletons consisting of loose spicules that fell apart after death, such as lyssacinosan hexactinellids and soft demosponges, usually have much poorer records. What is worse, these records are nearly exclusively represented by mixtures of spicules belonging to various taxa (see for example Hinde, 1880; Reif, 1967; Pisera, 1997, and literature therein). This does not mean, of course, that such sponges are not preserved intact at all. There are numerous examples of both demosponges (*Propachastrella* from the Upper Cretaceous; Schrammen, 1910-1912), or lyssacinosan hexactinellids having loose spicules (*Stauractinella* from the Upper Jurassic; Mehl, 1992; Pisera, 1997) whose preservation as body fossils was facilitated either by very early cementation and/or collagen cement. Another example is a rosselid sponge from the Upper Cretaceous of Denmark (Mehl, 1992). In the Eocene of Catalonia intact demosponges and hexactinellids with loose spiculation (Busquets et al., 1997; Pisera unpublished) are preserved,

most probably due to catastrophic burial. All these, however, are relatively rare cases showing only how much information is missing in the fossil record.

Some lyssacinosan hexactinellids may have entirely, or partly fused skeletons and such sponges are quite common among fossils, examples can include Triassic *Cypellosporgia* from the USA (Rigby & Gosney, 1983), *Hexactinoderma* and *Silesiasporgia* (Fig. 1C) from Poland (Pisera & Bodzioch, 1991), Cretaceous *Proeuplectella* from France (Moret, 1926) and *Regadrella* from Germany (Salomon, 1990) and Tertiary (Brimaud & Vachard, 1986b). The fusion in these sponges, however, is of irregular type (at points of contact and without formation of dictyonal strands; Fig. 1C), and happens rather late in ontogeny, in opposition to Hexactinosa and Lychniscosa where the fusion is an early ontogenetical phenomenon. I will not refer to these unusual sponges any further.

STRATIGRAPHICAL DISTRIBUTION OF HEXACTINOSA, LYCHNISCOSA AND LITHISTIDA

HEXACTINOSA. Hexactinosa are hexasterophoran hexactinellids having skeletons fused in a regular way, i.e., particular hexactines form longitudinal dictyonal strands (Reid, 1963) (Fig. 1B, D) (fusion of hexactines happens by

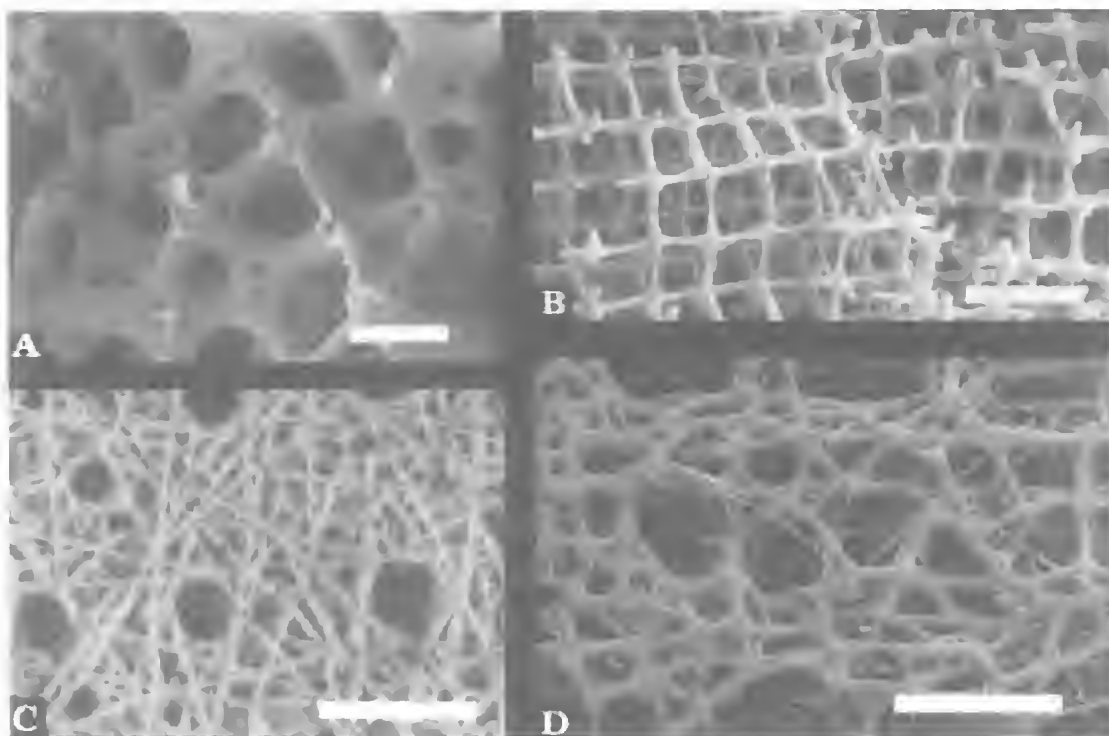


FIG. 1. Skeletons of hexactinellid sponges. A, Lychniscosan choanosomal skeleton, *?Rhogostomium* sp., Late Jurassic, Germany, (scale bar 200 μ m). B, Hexactinosan choanosomal skeleton (note that hexactines are fused together with the help of silica cement), *Sphenaulax* sp., Late Jurassic, Germany, (scale bar 500 μ m). C, Surface of lyssacosan choanosomal skeleton (note the irregular fusion of spicules which are mostly diactines), *Silesiaspongia rimosa* Pisera & Bodzioch, Middle Triassic, Poland, (scale bar 1mm). D, Hexactinosan choanosomal skeleton, *Dactylocalex* sp., Recent, (scale bar 1mm).

joining two rays into a common silica envelope). Fusion between particular strands may be less regular. For a long time Hexactinosa were regarded as a typical Mesozoic group (see Rigby, 1983); during the last several years, however, numerous reports appeared about the presence of this group in Devonian rocks (Rigby et al., 1981). Much earlier reports of their presence in the Paleozoic (Fraipont, 1911; Mayr, 1930) have been mostly overlooked.

The best and the richest fauna of these sponges I know so far is from the Late Devonian (Frasnian) of the Holy Cross Mountains in Poland (Rigby et al., 1981, and in prep.). These sponges are already very close to Jurassic and Cretaceous representatives of Hexactinosa, which suggests that they have an even longer, but unfortunately unknown Paleozoic history. (There is a chance that some sponges described in the literature from the Ordovician as belonging to sphaerocladine lithistids are in fact Hexactinosan sponges. It is their extremely regular structure,

typical of Hexactinosa, but unknown in lithistids, which suggest such a possibility. We know of both fossil and Recent hexactinosan sponges, that have enlarged spherical nodes. This problem needs further study). Smaller faunas of Devonian hexactinosans were reported from Germany, Belgium and Australia. There is a large gap between this late Devonian fauna and the next undoubted hexactinosans that occur only in the Mesozoic.

Undoubted Triassic hexactinosan sponges occur in Sichuan, China, Caucasus and in the Alps (Keupp et al., 1989; Wend et al., 1989; Boiko, 1990; Rigby et al., 1998). It is interesting that some of them belong to genera established from the Upper Jurassic. Among them are characteristic genera *Casearia* and *Sphenaulax*.

Hexactinosa become very diversified and common starting from the Late Jurassic (Schrammen, 1936-37; Trammer, 1982, 1989; Mehl, 1992; Pisera, 1997, and literature therein).

For example, a Late Jurassic fauna of Hexactinosa from the Swabian Alb is composed of at least of 23 genera and 48 species (Pisera, 1997). Rich hexactinosan faunas are known from the Early Cretaceous (Lagneau-Hérenger, 1962) and Late Cretaceous of Europe (Schrammen, 1910-1912; Moret, 1926). Tertiary hexactinosans are infrequent and reported mostly in recent times (Rigby, 1981; Rigby & Jenkins, 1983; Brimaud & Vachard, 1986b; Busquets et al., 1997). Today hexactinosans form important and diversified elements of deep-water sponge faunas mainly in tropical areas, and include about 40 genera and 135 species (Reid, 1968, and literature therein).

LYCHNISCOSA. Lychniscosan sponges also display development of dictyonal strands and fusion of spicules, but they have lychnisc (octahedral) nodes (Fig. 1A), in contrast to the solid nodes of hexactines in Hexactinosa. Their history is quite different. There is no trace of this group before the Middle Jurassic. Earlier reports of Triassic lychniscosan sponges (Vinassa de Regny, 1911; Keupp et al., 1989; Wendt et al., 1989; Wu Xi Chun, 1990) were proven to be erroneous (Mostler, 1990; Pisera & Bodzioch, 1991; Mehl, 1992). Also the report of Early Jurassic lychniscosans (Broglio Loriga et al., 1991) seems very doubtful.

The oldest known bodily preserved lychniscosan sponge (Pisera, 1993, and in prep.) belongs most probably to the Late Jurassic genus *Pachyteichisma* and occurs in the uppermost Bajocian of the Mečsek Mountains in southern Hungary. This genus is common in the Callovian of Kutch, India (Mehl & Fürsich, 1997, referred to as *Sporadopyle*) and it occurred also during the Late Jurassic (Pisera, 1997).

Lychniscosan sponges are an important part of the large Late Jurassic fauna from the Swabian Alb (34 species and 15 genera; Pisera, 1997) and Upper Cretaceous faunas of Northern Germany (81 species and 34 genera; Schrammen, 1912). Even if there is an 'oversplitting' of taxa this diversity is impressive, especially when compared with Recent diversity of this group.

For a long time very little was known about Tertiary lychniscosan sponges, and only one genus, *Manzonina* from the Miocene of Italy and Spain, was known. To this Pomel's genus *Pachychlaenium* (= *Tremabolites*) was added by Mehl (1992). More recent discoveries in the Eocene of Catalonia (Pisera in prep.) show that their diversity was lower than during the Late

Cretaceous, but was still higher than today, for they are represented there by at least 5-6 species and 5 genera, which are quite prevalent. Today, lychniscosan sponges are a relict group represented only by 3 species and 2 genera (Mehl, 1992) and are rare. The reason why Lychniscosa developed during the Cenozoic differently than the Hexactinosa remains unknown.

'LITHISTIDA'. Lithistids are demosponges characterised in having choanosomal skeletons composed of desmas joined by articulation without cementation by silica (Fig. 2A). There is no doubt that they are a polyphyletic group, and when we speak about 'lithistids' we should split them into smaller units that have the same geometry of desmas, with a greater probability of being monophyletic (i.e., Tetracladina Zittel, 1878, Rhizomorina Zittel, 1878, Dicranocladina Schrammen, 1924 (=Corallistidae Sollas, 1888), Sphaerocladina Schrammen, 1910, Megamorina Zittel, 1878 and Didymorina Zittel, 1878). Lithistids as a group are known from the Lower Palaeozoic (Rigby, 1983), and some Mesozoic groups, i.e., Rhizomorina (if the Palaeozoic rhizomorines are the same lineage as Mesozoic one), Sphaerocladina and Megamorina have their Palaeozoic representatives. The Dicranocladina are most probably closely related to Palaeozoic hindiids (Finks, 1971). Diversity of fossil and Recent lithistids, as a whole group, is probably comparable because in the Upper Jurassic of the Swabian Alb about 42 species have been found by me, whereas a Recent fauna of lithistids from the New Caledonia region is composed of 23 species according to Lévi & Lévi (1983). Taking into account that the Recent fauna represents only one time plane, the diversity may be regarded as similar. Diversity of particular groups, however, differs considerably. Tertiary lithistids, as a whole, are rather poorly known (Moret, 1924; Brimaud & Vachard, 1986a). For excellent and more detailed review of lithistids distribution than presented below see Wiedenmayer (1994).

The oldest bodily preserved Rhizomorina Zittel, 1878, characterised by irregular, usually thorny desmas called rhizoclonas (Fig. 2B-E), based on monaxons, are known from the Early Jurassic from Georgia (Nutsbidze, 1965), although rhizoclonic spicules are known from the Triassic (Wiedenmayer, 1994). Rhizomorine sponges are common only from the Late Jurassic on (Schrammen, 1910-1912, 1937; Moret, 1924; Brimaud & Vachard, 1986a; Pisera, 1997). They are probably the most common group of

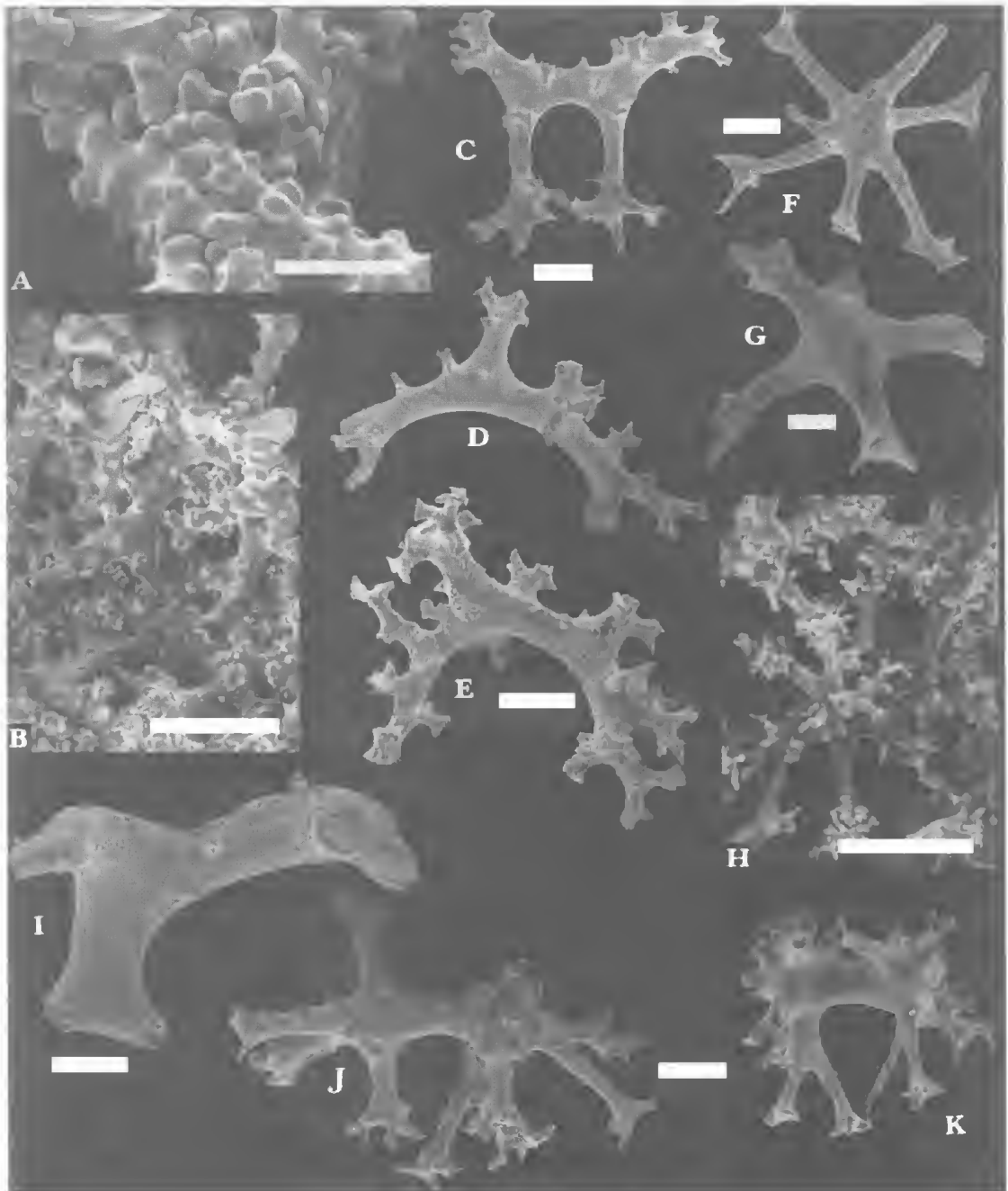


FIG. 2. Lithistid sponge spiculation; A, Articulation of desmas (note that desmas are joined only by articulation without cementation), Recent tetractinellid lithistid, Caribbean, (scale bar 100 μ m). B, Choanosomal skeleton of Recent rhizomorine sponge *Setidium* sp., (scale bar 200 μ m). C-E, Desmas (rhizoclones) of the Late Jurassic rhizomorine sponges, Germany, (scale bars 100 μ m). F-G, Desmas of the fossil sphaerocladine sponges, Late Jurassic, Germany, (scale bars 100 μ m). H, Choanosomal skeleton of the Recent sphaerocladine lithistid *Vetulina* sp., Caribbean, (scale bar 100 μ m). I, Desma (megaclone) of fossil megamorine sponge, Late Jurassic, Germany, (scale bar 100 μ m). J-K, Desmas (didymoclones) of fossil didymorine lithistid *Cylindrophyma* sp., Late Jurassic, Germany, (scale bar 100 μ m).

Mesozoic lithistids known in Europe. Rhizomorines are quite common in the Tertiary (Moret, 1924), and today they are represented by 8-10 genera.

Bodily preserved Tetracladina Zittel, 1878, characterised by usually regular desmas based on a tetraxon called tetraclone (Fig. 3F-G), already exist in the Triassic (known from the thin sections only; Keupp et al., 1989), but they are rare. They become common only in the Late Jurassic (5 genera and 6 species), with maximum fossil diversity in the Late Cretaceous where Moret (1926) cited 26 genera and 62 species from France alone. In Recent seas they are also common and represented by about 130 described species worldwide (Wiedenmayer, 1994 and the literature therein). In more restricted areas like New Caledonia 23 species and 16 genera were reported (Lévi, 1991).

The earliest Dicranocladina Schrammen, 1924, characterised by regular strongly tuberculated, usually tripodal or tetrapodal, desmas (Fig. 3A-E), based on monaxons, are known from 5 species and 3 genera of the Late Jurassic. They are distinguished with difficulty from Recent ones. Dicranocladina diversity is high in the Late Cretaceous (Moret, 1926, lists 8 genera and 15 species). Tertiary Dicranocladina are rarely reported (Rigby, 1981; Brimaud & Vachard, 1986a), but they are quite common in Recent seas (Lendenfeld, 1903; Levi & Levi, 1983; Levi, 1991).

The next group of lithistids, i.e., Megamorina Zittel, 1878 (which corresponds to Recent Pleromatidae Sollas, 1888), are characterised by desmas called megaclones (Fig. 2I). They appear as early as the Ordovician but their Mesozoic record starts in the Middle Triassic (Wiedenmayer, 1994, and literature therein). They become common and diversified in the Jurassic and Cretaceous (Schrammen, 1910-1912, 1937; Moret, 1926; Lagneau-Hérenger, 1962; Pisera, 1997). Their Tertiary record is poor and only one bodily preserved, recently discovered, but still undescribed species, has been found in the Eocene. Today Megamorina is also a small group with only 2 genera (Wiedenmayer, 1994).

Similar is the history of the Sphaerocladina Schrammen, 1910, which are characterised by desmas called sphaeroclones or astroclones (Fig. 2F-H). They first appear in the Paleozoic (Wiedenmayer, 1994, and references therein) (if astylospongiids are included here, and that may be

questioned), but their Mesozoic record starts in the Late Jurassic (3 genera and 5 species). Sphaerocladina have the same diversity in the Cretaceous (Moret, 1926, lists 3 genera, 5 species). They have a poor Tertiary record, and in Recent seas are represented most probably only by *Vetulina stalactites* Schmidt (Fig. 2H). This species has been suggested to be the rhizomorine (Gruber, 1993), but more recent studies of the holotype suggests that it is not.

The last group to be considered is Didymorina Zittel, 1878, with desmas called didymocones (Fig. 2J-K). They are extinct and undoubted representatives occur only in the Middle and Late Jurassic - 2 genera and 3 species. Similar loose spicules of uncertain affinity were reported by Mostler (1976) from the Triassic.

PATTERNS IN THE HISTORY OF SILICEOUS SPONGES WITH RIGID SKELETON.

Longevity of sponge genera. It has been known long that numerous Recent hexactinellid genera are long ranging and occur even in Upper Cretaceous rocks. For example Mehl (1992) found that of 31 genera from the Late Cretaceous Hexactinosa, 11 survive in Recent seas. The hexactinosan genus *Laocoetis* (= *Craticularia*) ranges most probably from the Early Jurassic (Nutschidze, 1965) until today (Lévi, 1986) - a duration of nearly 200 million years. The Recent genus *Dactylocalyx* has been reported by Trammer (1989) from the Late Jurassic. Recently discovered sponge faunas strengthen this pattern by showing the presence of the genera known from the Upper Jurassic also in the Triassic (e.g., the hexactinosan *Casearia* and *Sphenaulax*; Rigby et al., 1998), and other Cretaceous genera in the Tertiary (e.g., the lychniscosan *Becksia*, *Sporadoscinia*, *Brachiolites* in newly discovered Eocene faunas from Spain; Pisera, unpublished), thus pointing to the extremely conservative nature of these sponges at the generic level.

Lithistids also include several long ranging genera. *Cnemidiastrum*, for example, is typical of the Upper Jurassic but has been recently recorded in the Miocene, while the Cretaceous genus *Aulaxinia* has been discovered by Lévi & Lévi (1988) in Recent waters around New Caledonia. The Recent rhizomorine genus *Amphibleptula* from the Atlantic has been recognised in the Late Jurassic (Pisera, 1997). Numerous lithistids of the Late Cretaceous (especially rhizomorine sponges) show no recognisable differences when compared with Late Jurassic forms. It seems that different names given to these different faunas

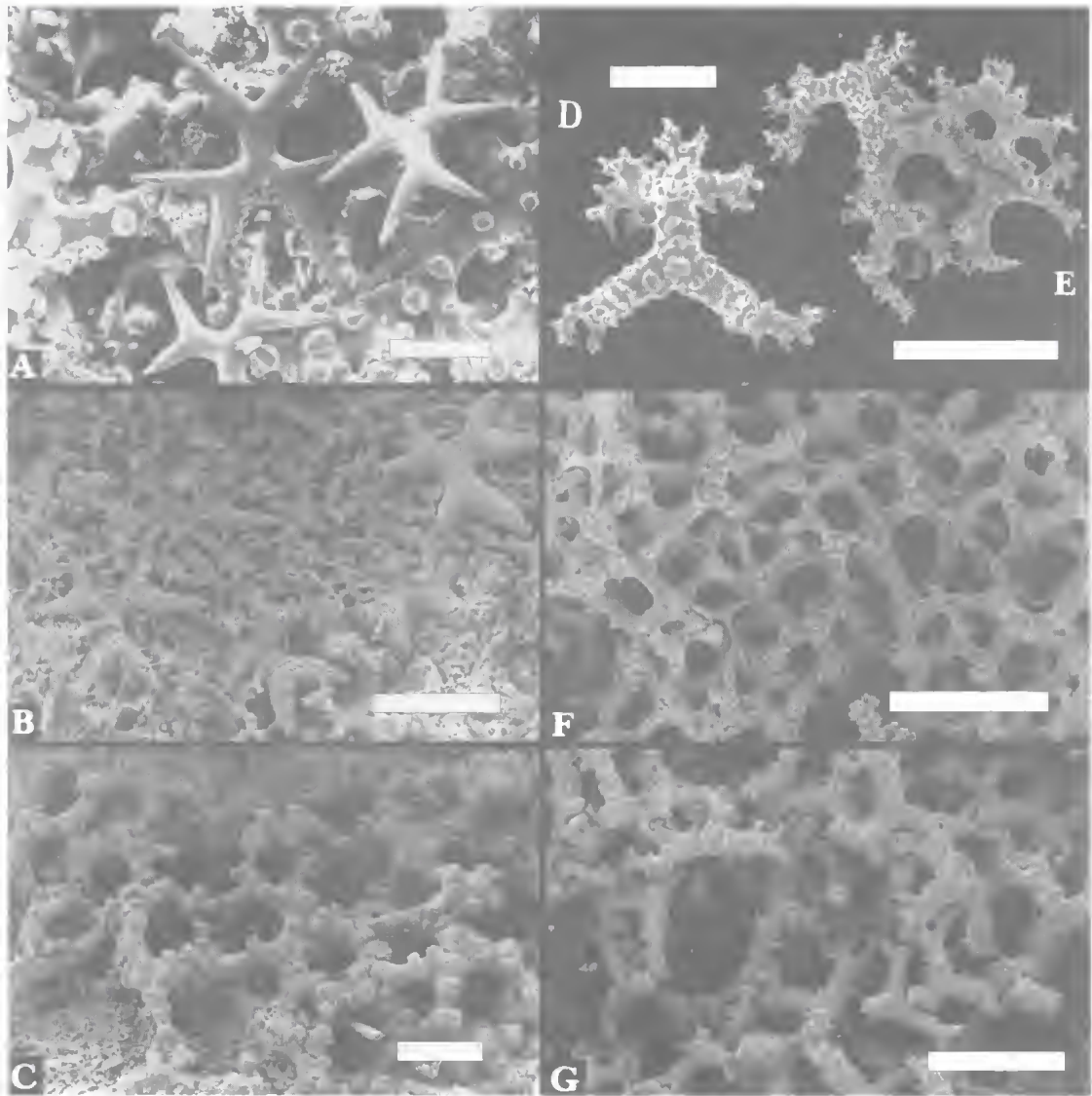


FIG. 3. Lithistid sponge spiculation; A, Recent *Corallistes* sp., choanosomal skeleton composed of strongly tuberculated dicranoclones, and dermal dichotriaenes, Gulf of Mexico, (scale bar 100 μ m); B-E, Fossil *Dicranoclonella* sp., Late Jurassic, Germany. B, Upper surface showing dermal dichotriaenes and rhizoclone-like modified dicranoclones between them, (scale bar 200 μ m); C, Choanosomal skeleton composed of strongly tuberculated dicranoclones, (scale bar 200 μ m); D, Isolated typical dicranoclone, (scale bar 200 μ m); E, Fragment of choanosomal skeleton, (scale bar 500 μ m). F, Choanosomal skeleton of Recent tetracladine sponge, Carribean, (scale bar 500 μ m); G, Choanosomal skeleton of fossil tetracladine sponge, Oligocene, the Ukraine, (scale bar 500 μ m).

stem from the philosophy that large age differences are enough to justify establishing a new genus. This approach is questionable. It appears that lithistids are also rather conservative and slowly evolving.

Sponges and K/T boundary. The Cretaceous-Tertiary (K/T) boundary was a time when most fossil groups of marine organisms were severely decimated. The pattern of distribution of siliceous sponges with rigid skeleton across this boundary is interesting. There are no sponge

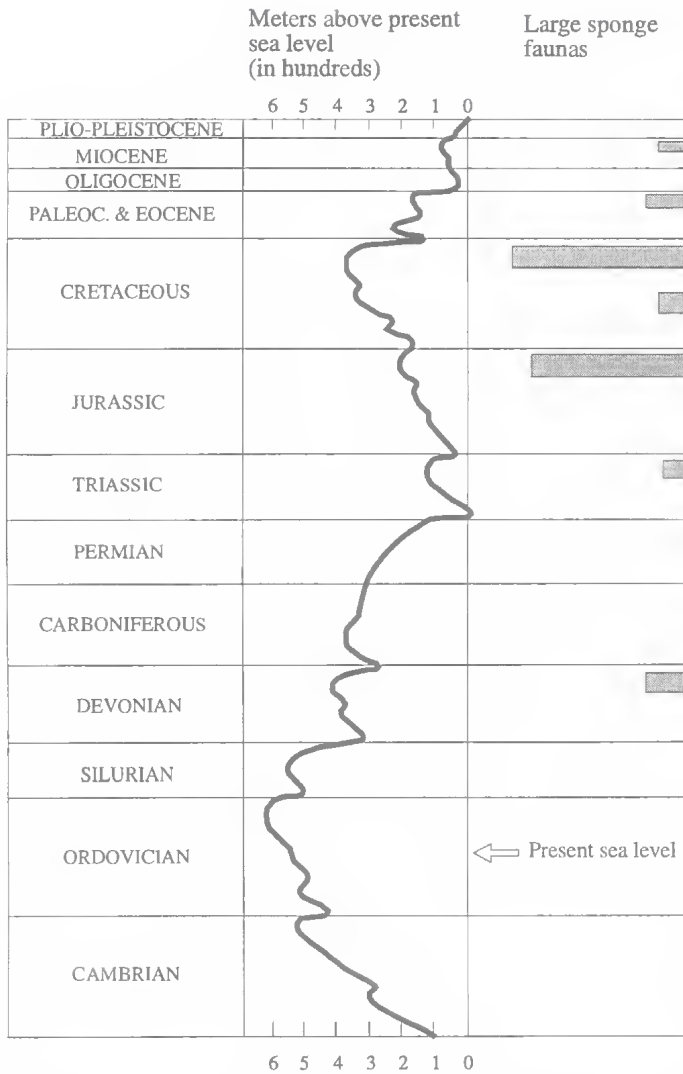


FIG. 4. Sea level curve for the Phanerozoic and the distribution of large faunas of siliceous sponges (sea level curve from Hallam, 1992).

faunas known directly above the boundary, but when one considers the newly discovered Eocene faunas from the Pyrenees (Busquets et al., 1997) composed of both lithistids (mostly tetractinellids, one megamorine and some rhizomorine sponges have been also found; Pisera, unpublished data) and hexactinellids with rigid skeletons, including both hexactinosans and lychniscosans. Such characteristic forms as *Guettardiscyphia*, a typical Cretaceous hexactinosan, are important elements (rock forming in places) of these Eocene faunas. Among lychniscosan sponges the so called

meandrispongids (*Brachiolites*, *Plocoscyphia*), and *Sporadoscinia*, which are characteristic of the Late Cretaceous, dominate the Eocene faunas (Pisera, unpublished data). A similar fauna has been reported also from the Eocene of the USA (Rigby, 1981; Finks, 1983, 1986). Miocene faunas from Algeria, described by Moret (1924), and from Spain described by Brimaud & Vachard (1986a, b) have many Mesozoic elements. Recent faunas of sponges with rigid skeleton are also considered by Reid (1967) as of the Tethyan (Mesozoic) origin. All this indicates that sponges were less strongly affected by K/T boundary disturbances than other organisms.

How to explain such behaviour of the siliceous sponges discussed here? It follows because they are (and were) rather deep-water creatures. They were at least probably protected by a water column from disturbances occurring at the surface. The rather simple character of sponges, which fed on colloidal matter and bacteria, may have also played a role, for they were less influenced by supposed disturbances of the food chain during the K/T event (whatever its cause). On the other hand, it is difficult even to speculate at the moment, upon what

differences, other than chance, caused different behaviour of particular groups of sponges (like *Hexactinosa* and *Lychniscosa*) in relation to K/T boundary event.

Large sponge faunas. So far I have been concentrated on the stratigraphic ranges of particular groups or lineages of sponges, but there are some interesting patterns in distribution of large sponge faunas as such. In this context large sponge faunas refer to faunas that are diverse, have wide geographical distribution, and in which sponges occur in profusion, where

sponges are usually a rock forming element. During the Late Jurassic, for example, they formed biostromal or reefal structures, and the sponge facies extends across the whole Europe from Portugal to Romania (Trammer, 1982, 1991; Leinfelder et al., 1994; Krautter, 1997; Pisera, 1997, and literature therein).

Distribution of large faunas of bodily preserved (intact) fossil sponges during the Meso-Cenozoic is rather punctuated and limited to certain periods of time. The largest such faunas known for a long time are associated with the Upper Jurassic, Upper Cretaceous, and the Miocene rocks (Fig. 4). Because of large gaps separating these faunas, they appear at the genus level to be composed of very different taxa, which makes interpretation of evolution of these sponges difficult. Such a pattern of distribution has been interpreted, at least for lithistids, by Rigby (1983) as the result of "selective preservation and discovery, not one of original limited diversity and density". This interpretation has partly found support in more recent important discoveries from the Late Triassic (China - Wendt et al., 1989; Wu Xi Chun, 1990), Middle Jurassic (Spain - Scheer, 1988; Hungary - Pisera, 1993; India - Mehl & Fürsich, 1997), Eocene (Spain - Busquets et al., 1997) and Miocene (Spain - Brimaud & Vachard, 1986a, b) and a smaller one from the Oligocene (Antigua - Wiedenmayer, 1994; Ukraine - Pisera, unpublished). Generally, however, if we look at the distribution of large sponge faunas, the pattern of punctuated record is preserved. The largest are of Late Jurassic and Late Cretaceous age (across the whole of Europe); smaller ones occur in the Upper Triassic (The Alps, Sichuan), Middle Jurassic (Spain, France, Hungary, Kutch in India), Eocene (Spain, Italy, Turkey) and the Miocene (Algeria, Spain, Italy). When one compares all these occurrences with the sea level history (Fig. 4), a clear correlation appears: the occurrence of the large siliceous sponge faunas is correlated with the high sea level times during the Mesozoic and Tertiary (and it seems that this pattern is valid also for the Paleozoic in the case of Hexactinosa in the Frasnian/Famenian). It points to the importance of sea level in controlling distribution of large sponge faunas. This relationship, however, is mostly of environmental character, although some evolution, took place especially at the species level. The sponges considered here are deep-water creatures and their widespread development may be interpreted as a possibility to colonise new, vast, relatively deep-water areas.

These areas were not available during lower sea level periods, and when sponges of these groups existed only in relatively narrow refugia along continental and island slopes, as it is in many cases today. Such new areas of relatively deep-water were at a distance from shore, had low sedimentation rates and low hydrodynamic energy, and thus were suitable for sponge colonisation.

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Note added in proof.

Eocene sponge faunas should be supplemented with a lithistid fauna from the southern Western Australia (Pickett, 1983, and references therein), of which I was earlier unaware. After preliminary examination of a new collection of sponges from this region (thanks to Dr. P. Gammon, Canada) it seems to be the largest, the

most diversified, and the best preserved lithistid fauna of the Tertiary.

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